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Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids

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Investigations into mechanisms of resource partitioning are particularly suited to systems where nascent interactive behaviors are observable. Wolf (*Canis lupus*) recolonization of the Greater Yellowstone Ecosystem provided such a system, and we were able to identify behaviors influencing the partitioning of resources by coyotes (*Canis latrans*) and wolves. We observed coyote–wolf interactions immediately after wolf recolonization, when reemergent behaviors mediating the outcome of competitive interactions were detectable and mechanisms of spatial avoidance were identifiable. Although coyotes used the same space as wolves, they likely minimized risk of encounter by making adaptive changes in resource selection based on perception of wolf activity and potential scavenging opportunities. When exploiting carrion subsidies (i.e., wolf-killed ungulates), coyotes relied on social behaviors (i.e., numerical advantage in concert with heightened aggression) to mitigate escalating risk from wolves and increase resource-holding potential. By adapting behaviors to fluctuating risk, coyotes might reduce the amplitude of competitive asymmetries. We concluded coyotes do not perceive wolves as a threat requiring generalized spatial avoidance. Rather, the threat of aggressive interactions with wolves is spatially discrete and primarily contained to areas adjacent to carrion resources. DOI: 10.1644/09-MAMM-A-078.1.

Key words: aggression, *Canis latrans*, *Canis lupus*, coyotes, interaction, resource partitioning, risk assessment, social status, wolves

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It is almost axiomatic that coexisting species with an apparent potential to compete should exhibit differences in behavior that insure they compete little or not at all (e.g., Menge and Menge 1974; Pianka 1969; Robinson and Terborgh 1995). These manifest behavioral differences often are the basis for resource partitioning, perhaps the most commonly cited explanation of sympatry (e.g., Johnson and Franklin 1994; Kitchen et al. 1999). However, investigations of competitive interactions rarely delve deeper to identify behavioral mechanisms that might mediate when or how resources are partitioned. In part, this may reflect that ameliorative behaviors are well entrenched in systems where potentially competing species have co-occurred over long periods of time. That is, competition has already occurred, and all that is observable is that resources have been partitioned. Opportunities to observe interspecific interactions while avoidance behaviors are reemergent, although rare, are among the best ways—including experimental manipulation (Brown and Munger 1985) and monitoring population decline (Roemer et al. 2002)—to uncover mechanisms leading to coexistence. Fortunately, wolf (*Canis lupus*) recolonization of northern Montana and the Greater Yellowstone Ecosystem has provided such an opportunity; presumably naïve (Berger et al. 2001) coyotes (*Canis latrans*) must alter behaviors to promote coexistence with a competitively dominant canid.

Given similarities in niche breadth and social behaviors, the potential for coyote–wolf interactions should be great. Subtle behaviors may be responsible for mediating the outcome of interactions, which at times may appear ambiguous. For example, although wolves kill coyotes (Murray Berger and Gese 2007), they also provide significant food subsidies in the form of scavenging opportunities (Atwood and Gese 2008; Paquet 1991; Wilmers et al. 2003). As a result, coyotes have strong motivation to exploit the putatively hostile space where

wolf-provisioned carcasses are located. However, to realize a net benefit from scavenge subsidies, coyotes need to manage the risk posed by wolves. Where coyotes are habituated to wolf presence, they apparently have become adept at partitioning space (Fuller and Keith 1981; Paquet 1991; Switalski 2003) while increasing dietary overlap (Arjo and Pletscher 1999; Paquet 1992). Presumably, spatial partitioning is avoidance behavior (Mills and Gorman 1997) in response to the risk of interspecific killing (Palomares and Caro 1999), whereas increased dietary overlap most likely results from coyotes scavenging wolf-killed prey (Paquet 1992; Wilmers et al. 2003). Although seemingly incongruous, these results suggest that coyotes can perceive the risk associated with wolves as spatiotemporally dynamic. Seemingly irreconcilable results, such as partitioned space use relative to increased dietary overlap, may reflect a gradient of risk-sensitive responses by coyotes. This would suggest that, for coyotes, perception of risk and potential for reward drive a dynamic partitioning of space.

Prey kill sites are potential foci for intense contest competition between wolves and coyotes (Atwood and Gese 2008). Because of the palpable risk of injury or death, coyotes must become adept at assessing and managing risk when exploiting wolf-killed prey. Many factors must be evaluated when estimating the immediate risk of and response to interspecific strife with wolves, and the level of risk perceived should influence the decision of whether to flee (Lima and Dill 1990; Ydenberg and Dill 1986) or retaliate (Geist et al. 2005). For example, in cooperative African carnivores, numerical superiority partially mediates successful kleptoparasitism (Carbone et al. 1997; Cooper 1991). Also, numerical superiority is a primary determinant in the outcome of territorial transgressions between adjacent coyote packs (Gese 2001) and, as a result, indirectly influences access to space within territories. By logical corollary, differences in relative group sizes may be an important determinant in when and how coyotes decide to share space with wolves. The extent to which differences in group size can diminish or intensify fine-scale risk perception may prove critical to reconciling space-sharing by sympatric canids.

We investigated coyote spatial ecology in response to wolves in Montana's Madison Range. Broadly, our aim was to determine if, when, and where coyotes partitioned space relative to risk of encountering wolves and to identify mediating behaviors. We initially addressed a basic question: does the presence of wolves modify space-use decisions by coyotes? We predicted that coyotes would continue to share space with wolves but alter intensity of habitat use as the likelihood of encountering wolves increased. Because wolf-killed prey represented a highly valued resource subsidy, we predicted coyotes would be compelled to exploit these sites of intense wolf activity but partition space use temporally to avoid strife with wolves. Finally, we identified behavioral and environmental correlates facilitating coyote exploitation of prey kill sites. Elucidating mechanisms of sympatry between coyotes and wolves will be important in learning how competition might influence canid community structure.

Materials and Methods

Study site.—We conducted the study in the Northern Madison Study Area (NMSA; 680 km^2), located in southwestern Montana's Madison Range of the Rocky Mountains, during the winters (December–April) of 2003–2005. The NMSA is approximately 50 km northwest of Yellowstone National Park and is bordered on the east by the Gallatin River, the west by the Madison River, and the south by the Spanish Peaks of the Gallatin National Forest. Shrub-steppe habitat (535 km^2) dominates valleys and benches on the NMSA; coniferous forest (145 km^2) comprises approximately 23% of the remaining area. Elevations range from 2,500 m in the Spanish Peaks to 1,300 m on the Madison River floodplain, and contribute to an ecological gradient varying from dry grassland–juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High-elevation dry sites occur on southern exposures and ridgelines and are predominantly mountain big sage (*Artemisia tridentada vaseyana*)–grassland mosaics. Temperatures range from highs of 21–32°C in the summer months to lows of −34°C in the winter months (Whitlock 1993).

A single wolf pack (Bear Trap pack) recolonized the NMSA in the winter of 2002–2003, representing the recolonizing front of wolves in the Madison Range. Bear Trap pack size ranged from 2 to 8 individuals, 1 of which (yearling female) was radiocollared and subsequently dispersed. Over the duration of the study the Bear Trap pack averaged 5 individuals; the same breeding pair was present for the duration of the study. Coyotes were distributed over the entire NMSA, and resided in multigenerational packs. Prewhelping pack size was 4 adults, and average litter size was 6 pups. Coyotes were subjected to hunting, and it was estimated that approximately 20% of the population was killed annually (Atwood and Gese 2008).

Capture and monitoring.—We captured and radiocollared coyotes in fall and winter 2003–2004 using padded foothold traps and aerial net-gunning. We located focal coyotes using ground-based radiotelemetry and then collected spatial data from continuous snow-tracking bouts. We considered radiotelemetry locations separated by 24 h to be spatially independent, so we calculated the mean Euclidean distance between a subset of those locations and used the resulting distance (630 m ± 127 *SE*) as the interval to sample habitat characteristics while snow tracking. For wolves, we collected spatial data during continuous snow-tracking sessions in which we initially searched for tracks by bisecting expected travel routes or backtracked from prey kill sites. To address concerns of autocorrelation we sampled habitat characteristics of point locations of wolves at 840-m intervals (Bergman et al. 2006). At each independent snow-track point, we recorded slope (°), elevation (m), aspect (classified as 4 cardinal directions), vegetation type, coyote group size, presence of wolf tracks, and wolf group size. We defined an encounter between coyotes and wolves as the spatial intersection of

coyote and wolf tracks. Because the spatial intersection of coyote and wolf snow tracks does not always represent a true temporal encounter, we relied on evidence of a chase to differentiate between spatial and temporal encounters. Additionally, continuous snow-tracking sessions were initiated within 24 h of snowfall to ensure that intersecting coyote and wolf tracks reflected potential spatial interaction over a relatively short timescale.

We located prey kill sites while snow tracking wolves. Once a kill was located, we confirmed predation as the cause of death (Atwood et al. 2007) and recorded data on habitat attributes (i.e., cover type and topography) and canid tracks present. If coyotes and wolves were feeding at kill sites, we collected observational data on interactive behavior. We observed activity via 15–45× spotting scopes, recording canid group sizes, social status of individuals present, time spent feeding (T_{acc}; carcass access time in min), and stage of carcass consumption (Wilmers et al. 2003). We entered kill-site locations into a geographic information system to quantify the number of wolf-killed prey located within coyote and wolf pack home ranges and core areas, and for subsequent analyses to identify factors influencing the probability of spatial and temporal encounter between coyotes and wolves. Research and handling protocols followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committee at the National Wildlife Research Center (QA-1147).

Spatial segregation, resource selection, and interaction.— We estimated the extent of spatial segregation between coyotes and wolves by measuring spatial overlap and congruence in utilization distributions (UD) of 95% fixed-kernel (FK) home ranges and 60% FK (Shivik et al. 1996) core areas. We used FK estimators with least-squares cross validation because they are better able to differentiate discrete centers of activity than are adaptive kernel estimators (Kernohan et al. 2001). We quantified overlap of home ranges and core areas using theme-overlay routines in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). We calculated overlap as:

$$\text{percent overlap} = [(\text{coyote-wolf home-range overlap})/\text{coyote home range}] \times 100. \quad (1)$$

However, in isolation, spatial overlap can be a poor indicator of interaction because kernel contours represent only the outline of an accumulated areal distribution. That is, important information on intensity of use of shared space can be lost unless the distributions of point locations within overlapping contours are considered. Therefore, we also assessed spatial segregation by measuring the congruence of UDs for overlapping coyotes and wolves by using the UD overlap index (UDOI) developed by Fieberg and Kochanny (2005):

$$\text{UDOI} = \text{A}_{i,\text{wolf}} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \widehat{\text{UD}}_i(\text{x,y}) \times \widehat{\text{UD}}_{\text{wolf}}(\text{x,y}) d\text{x}d\text{y}, \quad (2)$$

where $\text{A}_{i,\text{wolf}}$ is the area of overlap between the focal coyote pack and the Bear Trap wolf pack, and $\widehat{\text{UD}}_i$ and $\widehat{\text{UD}}_{\text{wolf}}$ are the estimated utilization distributions for the *i*th coyote pack and the wolf pack, respectively (Berger and Gese 2007). UDOI values <1 indicate little congruence in UD, whereas values >1 indicate greater congruence in overlapping UD. We estimated home ranges, core areas, and percentage overlap using the animal movement extension (Hooge et al. 1999) and overlay routines in ArcView. We calculated UDOI values in program R (http://www.r-project.org).

We developed resource selection function (RSF—Manly et al. 2002) models by choosing 3 random points to represent resource availability for every independent animal location. We selected random points from circular buffers centered on individual locations (Arthur et al. 1996; Johnson et al. 2006) with radii equal to the respective snow-tracking sampling interval (630 m for coyotes and 840 m for wolves). Resource use and availability were related to 6 categorical cover type variables (conifer, juniper, riparian, grassland, shrub-steppe, and aspect) and 5 continuous variables (distance from road and water features in meters, elevation in meters, slope in degrees, and snow depth in centimeters). We modeled categorical habitat and aspect variables using dummy variable coding, excluding reference categories. We pooled location data across individuals to develop population-level RSF models of use versus availability of habitat attributes for coyotes and wolves at the home-range scale. RSFs were estimated via logistic regression. Following Manly et al. (2002) we dropped the intercept and denominator from the logistic equation and all RSF models took the form:

$$\text{w}(\text{x}) = \exp\left(\sum \beta_i \text{x}_i\right), \quad (3)$$

where *i* refers to landscape variables 1 through *n* for used (obtained through snow tracking and direct observation) and available random locations. We started with global models, and variables were evaluated and retained using a backward stepwise procedure. We then used Akaike information criterion with a small sample size correction factor (AIC_C) to rank candidate models based on Akaike weights (w_is—Burnham and Anderson 2002) and selected top-ranked models of coyote and wolf resource selection at the home-range scale.

In addition to comparing resource selection between coyotes and wolves, we wanted to determine whether coyotes altered intensity of resource use whether inside or outside of wolf core areas (60% FK) and in response to risks of spatial and temporal encounters with wolves. To make that determination we needed to assemble models with consistent variables, and variance–covariance matrices (Hosmer and Lemeshow 2000), so that regression coefficients could be directly compared between models. Thus, using our previously ranked candidate models of coyote and wolf resource selection within home ranges, we followed Burnham and Anderson (2002) and used the sum of all w_i for each variable to rank them in order of importance. We then selected a consistent set of variables for inclusion in our models of coyote resource

selection when inside or outside of wolf core areas and for risk of spatial and temporal encounter. For models of resource selection inside and outside of wolf core areas we defined availability using the same method as home-range–scale RSF models. Because our data set also consisted of coyote spatial locations and the fraction of locations resulting in spatial and temporal encounters, we extended our use of RSF to estimate the conditional relative risk of spatial and temporal encounter given use of habitat attributes. We coded encounter locations as ''used'' and locations where no encounters occurred as ''unused.'' When data consist of known encounters, the used–unused distinction corresponds to a true probability function (RSPF), and conditional relative risk of a spatial or temporal encounter given use is expressed in the full logistic form:

$$p(\mathrm{x}) = \left[\exp\left(\beta_0 + \sum \beta_i \mathrm{x}_i\right) / 1 + \exp\left(\beta_0 + \sum \beta_i \mathrm{x}_i\right)\right], \quad (4)$$

where i refers to landscape variables 1 through n for encounter and use locations. Unlike equation 3, the intercept is included because the sampling probability is known and a true probability function is estimated (Manly et al. 2002).

Finally, we used generalized linear mixed models (Proc Glimmix, SAS 9.3; SAS Institute, Cary, North Carolina) to model coyote access time (T_{acc}) at carcasses as a function of year, coyote social status, prey type, cover distance, stage of carcass consumption, snow depth at kill site, and the difference between coyote and wolf group sizes. This method enabled the fitting of random terms and therefore accounted for repeated sampling across error terms. Because we sampled some of the same individuals repeatedly, we included individual and coyote pack as random factors in the models with 1st-order autocorrelation as a covariance structure. We used restricted maximum-likelihood methods for model estimation and Satterthwaite's F-tests to gauge effects (McCullagh and Nelder 1991). Year was included as a variable in generalized linear mixed models because we suspected that, over time, coyotes could have learned to better manage the risk of scavenging wolf-killed prey, resulting in greater carcass access time.

For all logistic regression analyses we checked continuous variables for conformity to linearity using the quartile method (Hosmer and Lemeshow 2000) and for collinearity using correlational analysis (we eliminated any one of a pair of variables with Pearson $r \leq 0.30$). We ensured final model fit by testing with the Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 2000). We evaluated predictive performance of models using k-fold cross validation (Boyce et al. 2002), where we partitioned the model data set following a test-to-training ratio of 20% (i.e., 5 subsets). Finally, we assessed predictive capacity using Spearman rank correlations (r_s) between grouped training and test data (Fielding and Bell 1997). We used AIC_C to determine which parameters were to be retained in all regression models; we considered AIC_C values that exceeded 4.0 to be significantly different (Burnham and Anderson 2002). We used Akaike weights (w_i) to gauge relative importance of factors influencing carcass access time, and used the evidence ratio of the ΔAIC_C weights for model i and model j as the likelihood that model i was better than model j.

Results

We captured and radiocollared 29 coyotes, 21 of which were residents belonging to 11 packs. We monitored the same 11 packs (prewhelping group size: $\bar{X}$ = 4 adults ± 0.2 *SE*) over both winters, although within-pack composition changed slightly. Over the 2 winters, we tracked coyotes for 1,603 km ($\bar{X}$ = 72.86 km per pack ± 4.69 *SE*) and wolves for 518 km. Backtracked coyotes intersected 97 sets of wolf tracks (excluding encounters at kill sites) and followed those tracks in a forward direction for an average of 4.2 km. We located 92 wolf kill sites, 77 (85%) of which were visited by coyotes. All monitored coyote packs visited ≥2 wolf kill sites ($\bar{X}$ = 5.6 per pack ± 1.2 *SE*). On 22 occasions, coyotes forward-tracked wolves to prey kill sites. One collared adult coyote (beta female; Little Lamar pack) and 2 uncollared pups (6–11 months old) were found killed by wolves; by comparison, 3 collared adults were killed by cougars (*Puma concolor*). All coyote mortalities attributed to interspecific killing occurred near (≤200 m from carcass) prey kill sites.

Winter home-range size for coyotes averaged 11.09 km^2 ± 1.03 *SE*, and core areas averaged 2.70 km^2 ± 0.29 *SE*. Wolf home-range size was 484.61 km^2 with combined core areas of 72.38 km^2. Percent overlap of coyote home ranges by the Bear Trap pack was extensive in both winters (95% FK: $\bar{X}$ = 78% ± 5.5% *SE*; 60% FK: $\bar{X}$ = 82% ± 6.7% *SE*). In 2003–2004 portions of 8 coyote home ranges and 3 core areas (Fig. 1a) fell within 2 wolf core areas (60% FK); in 2004–2005 portions of 7 coyote home ranges and 5 core areas (Fig. 1b) fell within 4 wolf core areas. Coyote and wolf UD within overlap areas deviated from uniform, ranging from 0.11 to 0.47 for home ranges (95% FK: $\bar{X}$ = 0.29 ± 0.08 *SE*), and from 0.00 to 0.21 for core areas (60% FK: $\bar{X}$ = 0.12 ± 0.03 *SE*).

Resource selection.—Correlation analyses indicated that distance to water and road features were positively correlated (n = 4,208 locations, $P < 0.001$, $r = 0.67$). We chose not to include distance to water in RSF models because distance to road features explained a greater portion of deviance. Despite some overlap in the variables retained in the best models of coyote and wolf home-range–scale resource selection, important differences were observed in the use of landscape attributes (Table 1). Probability of coyote occurrence increased in riparian (β = 1.558), grassland (β = 1.916), and shrub-steppe (β = 1.501) habitats, as did probability of wolf occurrence (riparian: β = 1.916; grassland: β = 0.766; and shrub-steppe: β = 1.688). Additionally, probability of wolf occurrence increased on south aspects (β = 0.956) and decreased in juniper-savanna habitat (β = −14.724). Despite small coefficient values, elevation (coyote: β = 0.003; wolf: β = −0.001) and distance from roads (coyote: β = −0.001; wolf: β = −0.0003) were retained in the top-ranked coyote

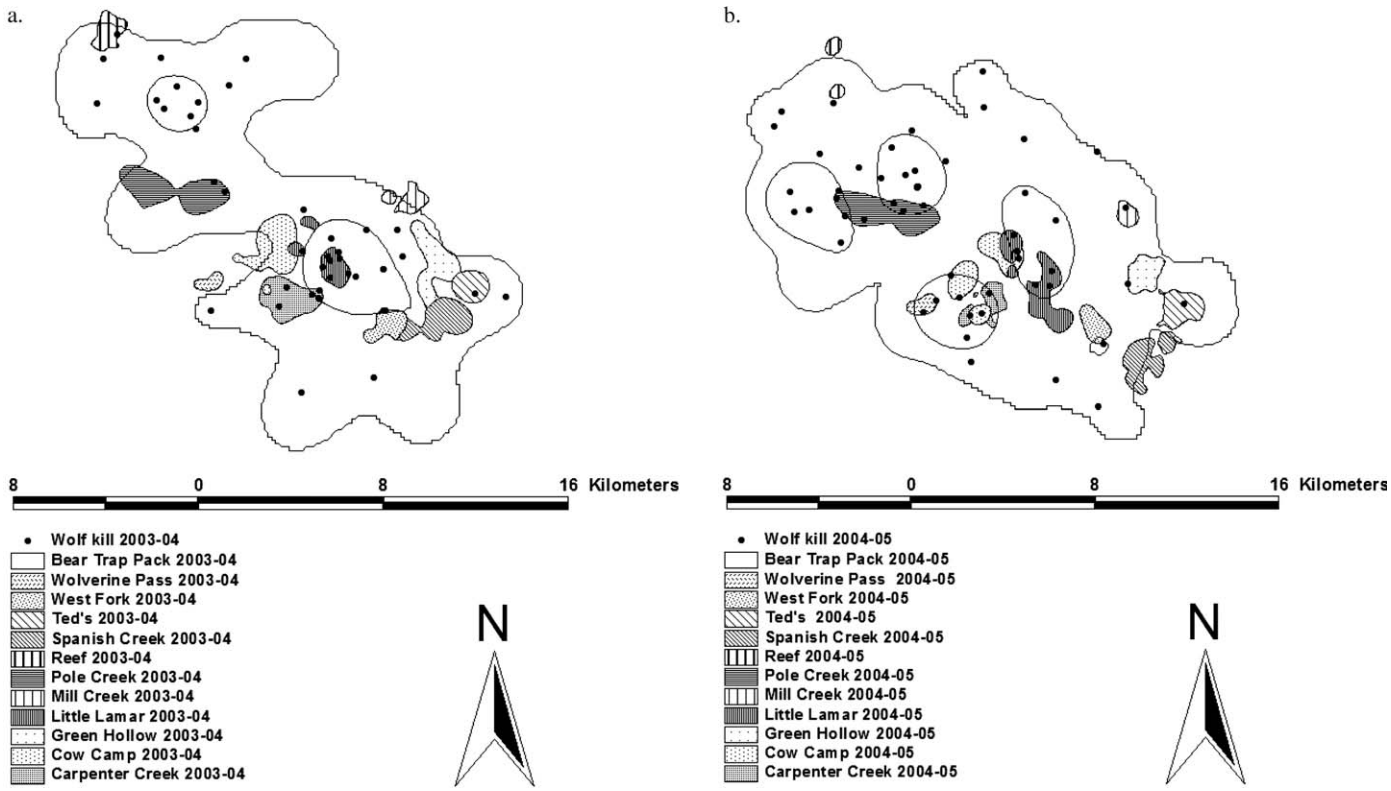

Fig. 1.—Overlap of coyote core areas (60% fixed kernel) with the Bear Trap pack wolf home range (95% fixed kernel) and core areas for the winters of a) 2003–2004 (with 2 wolf core areas) and b) 2004–2005 (with 4 wolf core areas) in the Northern Madison Study Area (NMSA), Montana.

and wolf models, and the average w_is (Table 2) suggested that the 2 variables influenced resource selection. All variables retained by the top-ranked model of home-range–scale resource selection by coyotes also were retained in the consistent-set RSF models of coyote resource selection inside and outside wolf core areas and the RSPF models of coyote–wolf encounter.

Based on the consistent-set models, coyotes altered the intensity of resource selection in response to escalating likelihood of encountering wolves. Comparison of odds ratios from RSF models of coyote resource selection inside and outside wolf core areas (60% FK) indicated that coyotes were approximately 1.41, 1.38, and 1.22 times more likely to use grassland, shrub-steppe, and riparian habitats, respectively, when outside wolf core areas (Table 1). Inside wolf core areas the conditional relative risk of a spatial encounter between coyotes and wolves increased approximately 87%, 81%, and 37% given use of riparian, shrub-steppe, and grassland habitats, respectively (Table 1). Although the conditional relative risk of a coyote–wolf temporal encounter increased 82% in riparian habitats, the risk decreased by 36% in grassland and 16% in shrub-steppe (Table 1). We found no pronounced differences in the relative odds of elevation and distance from roads among the constrained resource selection RSF and risk of encounter RSPF models (Table 1).

In all RSF models a strong majority of predictor variables were selected for, and models containing the top 5 variables were consistently ranked either 1st or 2nd (Table 2). Based on Hosmer–Lemeshow tests, all final models displayed adequate fit (Table 3). Spearman rank correlations from the *k*-fold cross validation indicated a strong relationship between the training and test data (Table 3). Given the above, we felt justified in using the consistent-set modeling approach to compare variables across RSF and RSPF models.

Interaction at ungulate carcasses.—We observed 52 individual coyotes (11 packs; 21 collared and 31 uncollared) scavenging in the presence of 6 individual adult wolves (all of known social status) for 681 h at the 77 ungulate carcasses. Fifty-six percent (n = 52) of all wolf kill sites were located within wolf core areas, which comprised, on average, 15% of the total area used by the Bear Trap pack. Forty-three percent (n = 33) of the wolf kill sites visited by coyotes also were located within coyote and wolf core areas. By contrast, 20% (n = 15) of wolf kill sites visited by coyotes were outside wolf core areas, and 12% of those fell outside monitored coyote pack boundaries. We witnessed 36 discrete bouts of agonistic interactions (i.e., spatiotemporal encounters) at 23 carcasses involving 6 different coyote packs and the Bear Trap wolf pack. Seventeen bouts ended with coyotes supplanting wolves from carcasses, all of which occurred when the carcass was nearly depleted. The effects of group size and stage of carcass consumption on mediating coyote access to carcasses was evidenced further by modeling results. The top-ranked model, T_{acc} = year + carcass stage + group difference, was ≈14 times more likely to be the

Table 1.—Relative odds ratios of parameter estimates, standard errors (*SE*s), and corresponding *P*-values for independent variables in resource selection function (RSF) models for coyote and wolf home-range resource selection, and consistent-set resource selection probability function (RSPF) models of risk of spatial and temporal encounter on the Northern Madison Study Area (NMSA), Montana, 2003–2005. *n* is the combined number of animal and random locations used in each analysis.

Model	*n*	Riparian	Grassland	Shrub-steppe	Juniper	South aspect	Elevation	Distance road
Coyote home range	10,160	4.751	6.791	4.484	—	—	1.002	1.000
SE		0.339	0.199	0.230	—	—	0.004	<0.001
P-value		<0.001	<0.001	<0.001	—	—	<0.001	<0.001
Wolf home range	2,464	19.948	4.792	3.466	0.194	2.088	0.968	1.000
SE		0.348	0.226	0.250	0.615	0.169	<0.001	<0.001
P-value		<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001
Coyote inside wolf core	6,998	10.910	6.479	2.589	—	—	1.000	0.999
SE		0.295	0.151	0.179	—	—	<0.001	<0.001
P-value		<0.001	<0.001	<0.001	—	—	0.691	<0.001
Coyote outside wolf core	3,162	13.364	9.124	3.582	—	—	1.001	0.999
SE		0.333	0.188	0.217	—	—	<0.001	0.001
P-value		<0.001	<0.001	<0.001	—	—	0.048	<0.001
Spatial encounter	1,043	36.885	10.715	23.755	—	—	0.995	0.998
SE		1.112	1.038	1.048	—	—	0.001	<0.001
P-value		0.001	0.022	0.002	—	—	<0.001	0.001
Temporal encounter	672	26.840	4.349	3.758	—	—	1.000	0.999
SE		0.494	0.386	0.416	—	—	<0.001	<0.001
P-value		<0.001	0.001	0.001	—	—	0.071	0.003

best candidate model than the 2nd model, T_{acc} = carcass stage + group difference + snow depth (Table 4). Access time at carcasses increased with increasing coyote group size (β = 2.06; Fig. 2), stage of carcass consumption (β = 1.19), and over successive years (β = 4.75).

Discussion

Our work indicated the following: coyotes did not segregate spatially from wolves but rather modified space use by displaying adaptive resource selection in response to escalating risk of encountering wolves; when wolf-killed prey were available, coyotes traded increased risk for scavenge benefits; and numeric superiority increased resource-holding potential for coyotes and may have functioned to lessen the potential for negative outcomes in interactions with wolves. The large proportion of wolf kills also located within coyote and wolf core areas (43%), along with extensive overlap, resulted in coyotes frequently traversing areas used intensively by wolves. Given that coyote core areas were relatively small, the concentration of scavenge resources and wolf activity created a situation where the likelihood of encounter was great. Coyotes, then, had to decide when and how to exploit these areas while minimizing the risk of aggressive interaction. If coyotes regarded wolves as a spatial threat, when presented with the opportunity, they would not have located

Table 2.—Akaike weights (w_is) for variables evaluated in resource selection function (RSF) and resource selection probability function (RSPF) models for coyote and wolf resource selection and encounter. Shown are the w_is for each variable averaged over all selection functions (coyote home range, wolf home range, coyote–wolf spatial encounter, and coyote–wolf temporal encounter) and the average rank of variable importance for the Northern Madison Study Area (NMSA), Montana, 2003–2005.

Variable	Coyote home range	Wolf home range	Coyote inside core	Coyote outside core	Encounter spatial	Encounter temporal	Average w_i	Average rank
Riparian	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1
Grassland	1.000	1.000	0.987	1.000	0.972	0.934	0.982	2
Shrub-steppe	0.993	0.881	0.787	0.991	0.947	0.713	0.885	3
Distance from road	0.964	0.789	0.841	1.000	0.826	0.809	0.871	4
Elevation	0.803	0.687	1.000	0.842	0.786	0.711	0.805	5
South aspect	0.527	0.874	0.431	0.526	0.451	0.497	0.318	6
Juniper	0.289	0.511	0.076	0.118	0.000	0.000	0.166	7
West aspect	0.069	0.000	0.060	0.000	0.015	0.011	0.026	8
Conifer	0.000	0.004	0.000	0.002	0.001	0.000	0.001	9
Snow depth	0.000	0.001	0.001	0.000	0.001	0.001	0.000	10
East aspect	0.001	0.001	0.000	0.000	0.001	0.001	0.000	10
North aspect	0.001	0.001	0.000	0.000	0.001	0.000	0.000	11

Table 3.—Model fit and assessment of ability to predict the relative probabilities of home-range resource selection by a) coyotes and b) wolves, resource selection by coyotes when c) inside and d) outside of wolf core areas, and risk of e) spatial and f) temporal encounter between coyotes and wolves on the Northern Madison Study Area (NMSA), Montana, 2003–2005.

Model	k_i	HL χ^{2a}	HL *P*-value	Likelihood ratio χ^2	Likelihood ratio *P*-value	*k*-fold cross validation, r_s
a. Coyote home range	5	10.81	0.195	691.08	<0.0001	0.91 ± 0.02
b. Wolf home range	9	5.46	0.707	119.49	<0.0001	0.84 ± 0.04
c. Coyote inside wolf core area	5	10.03	0.263	102.14	<0.0001	0.81 ± 0.02
d. Coyote outside wolf core area	5	11.45	0.178	106.05	<0.0001	0.83 ± 0.03
e. Spatial encounter	5	13.21	0.105	504.28	<0.0001	0.80 ± 0.04
f. Temporal encounter	5	10.70	0.219	703.86	<0.0001	0.77 ± 0.05

[a] Hosmer–Lemeshow chi-square statistic.

core areas in wolf activity centers. Rather, they would have avoided areas used intensively by wolves to reduce the threat associated with encounter. That coyotes did exploit these areas indicated that threat perception and avoidance behaviors were more nuanced.

As with other studies (Arjo and Pletscher 1999; Berger and Gese 2007), wolves were a source of mortality for coyotes on the NMSA. Yet despite the inherent risk, coyotes did not display avoidance of wolves: spatial overlap was great and resource selection was qualitatively similar. However, UDOI values were relatively low indicating differential use of overlap areas, and coyotes altered the intensity of habitat use as the risk of encountering wolves increased. For example, although coyotes and wolves both used riparian, grassland, and shrub-steppe cover types, the intensity of use by coyotes decreased when in wolf core areas. The decrease in intensity of use might have represented adaptive resource selection as coyotes altered use of certain cover types where risk of encountering wolves was greatest. The risk of spatial encounter in wolf core areas was greater than the risk of temporal encounter for all cover types, and it appeared that risk-sensitive resource selection by coyotes represented an attempt to partition resource use temporally rather than spatially. Coyotes are both predators and scavengers, and wolves represent not only a mortality risk but also an important provider of scavenge subsidies (Atwood and Gese 2008; Paquet 1992; Wilmers et al. 2003). Thus, rather than indiscriminately avoiding wolves, coyotes modified space-use decisions by altering the intensity of resource selection to balance the probability of lethal attack with the potential for energetic benefit.

Relationships between some sympatric species of canids have been portrayed in the context of obligate hostility, where body size mediates asymmetry and the larger species dominates (Carbyn 1982; Hersteinsson and Macdonald 1992; Major and Sherburne 1987; Rudzinski et al. 1982). In the aggregate these manifest outcomes of interaction may be the norm, but tacit acceptance of this general view may overlook important behavioral adaptations that facilitate sympatry. The potential for coexistence is not an all-or-nothing enterprise; ample research on niche partitioning in terrestrial mammals has confirmed that although interspecific competition frequently occurs, little evidence exists in support of competitive exclusion (Connell 1983; Schoener 1983). Our research indicates that, in most cases, wolves were able to exclude coyotes from carcasses and monopolize access until they decided to forego further feeding. However, evidence also suggested that coyotes, on occasion, could be successful in supplanting wolves from carcasses. Several factors played a critical role in determining whether coyotes were successful, chief among them being numeric superiority. When numerically superior, coyotes were more likely to engage wolves aggressively at carcasses, using harassment behaviors (e.g., barking and biting).

Condition-dependent superior vigor by a smaller species is not without precedent. Smaller-sized black-backed jackals (*Canis mesomelas*) routinely rely on aggression to displace larger side-striped jackals (*Canis adustus*) from prime foraging habitat (Loveridge and Macdonald 2002). Black-backed jackals also are more likely to risk feeding among lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) than are other species of jackals (Estes 1991; Mills 1990), and spotted hyenas are more successful in kleptoparasitizing lions when they can recruit sufficient clan members to appropriate a carcass (Honer et al. 2002). Vigorous displays of aggression can allow a smaller species to gain access to a resource that

Table 4.—Top-ranked multiple regression models of factors influencing access time (T_{acc}) for coyotes feeding on wolf-killed prey on the Northern Madison Study Area (NMSA), Montana, 2003–2005. Model structure is followed by estimates of partial regression coefficients and Akaike information criterion with a small sample size correction factor (AIC_C) values and weights of evidence (w_i).

Model	β_0	β_1	β_2	β_3	β_4	β_5	β_6	R^2	AIC_C	w_i	*P*-value
1. β_0 + group difference + carcass stage + year	−6.69	2.06	1.19	4.75	—	—	—	0.51	313.1	0.85	<0.001
2. β_0 + group difference + carcass stage + snow	0.54	2.01	1.29	0.10	—	—	—	0.46	318.4	0.06	<0.001
3. β_0 + group difference + carcass stage + social status + prey type + year − cover distance	−7.09	2.04	1.17	0.03	0.37	4.63	−0.002	0.48	319.6	0.04	<0.001

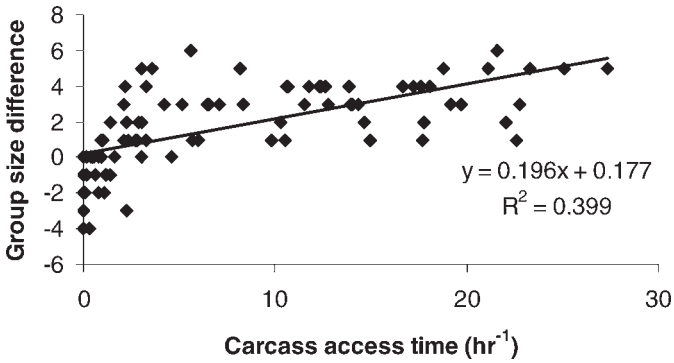

Fig. 2.—Relationship between difference in group size (no. coyotes − no. wolves) and carcass access time (T_{acc}) for coyotes scavenging wolf-killed prey in the Northern Madison Study Area (NMSA), southwestern Montana, 2003–2005.

might otherwise be monopolized by a larger competitor. Maynard-Smith and Parker (1976:159) termed this successful aggressive behavior by asymmetrically subordinate competitors ''resource holding potential.'' For coyotes, numeric superiority has been identified as a factor critical to the aggressive defense of carcasses and territorial boundaries against incursions by conspecifics (Gese 2001). Our study supports the notion that coyotes may rely on a similar strategy when exploiting wolf-killed carcasses, namely that, when numerically superior, they may forego temporal partitioning and attempt to supplant wolves from carcasses. Thus, despite the disadvantage of smaller body size, coyotes can demonstrate resource-holding potential, as measured by carcass access time (T_{acc}), when numerically superior to wolves. However, we caution that for coyotes, resource-holding potential is not solely a function of numeric superiority but rather is dependent on several factors.

Numerically superior coyote groups were able to feed at carcasses for a greater duration as the stage of consumption progressed. Foraging theory provides a contextual framework for understanding why access increased concomitant with the diminishing resource. If a prey kill site is analogous to a resource patch, then a forager should feed at that kill until the marginal value (Charnov 1976) of remaining falls below the expected value of realizing future caloric gains. Over time, handling time at a carcass increases as the ease of removing tissue decreases. Wilmers et al. (2003) characterized the stages of carcass consumption by wolves and found that as wolves progressed from feeding on organs to minor muscles, feeding rate increased while estimated biomass consumed decreased. This increase in carcass handling time, commensurate with a decrease in consumption, may make carcasses less valuable to wolves. As a result, wolves might be less inclined to mount a vigorous defense against kleptoparasitism by coyotes and more likely to leave the resource ''patch.'' The tipping point may occur when coyotes are numerically superior, and the energetic cost of defense by wolves is no longer balanced through ingestion of carcass biomass. Access time at carcasses also increased over successive years and could represent adaptive behavioral strategies by coyotes. That is, formerly naïve (Berger et al. 2001) coyotes might have learned, through previous experience, to exploit carcasses in the latter stages of consumption when wolf defensive vigor (and attendant risks to coyotes) wanes. It is plausible that coyotes might have learned, through both positive and negative reinforcement, to identify optimal conditions for exploiting wolf-killed prey. We encourage further investigation into the cognitive processes that can inform adaptive risk-sensitive behaviors.

Investigations into mechanisms of competition are particularly suited to systems where interactive behaviors are emergent, and wolf recolonization of the Greater Yellowstone Ecosystem provided a system where we were able to identify developing behaviors mediating competitive interactions between coyotes and wolves. Previous research has provided a solid foundation for characterizing sympatry between these canids by describing where and when space is partitioned (Arjo and Pletscher 1999; Paquet 1991; Switalski 2003). We built upon this foundation to elucidate a key behavioral mechanism mediating spatial partitioning: the risk perception–spatial avoidance nexus. In sum, coyotes relied on subtle behaviors to avoid spatial interaction with wolves and conspicuous behaviors to mitigate the outcome of temporal interactions. This would suggest that coyotes changed their behavior to reflect the ebb and flow of the wolf risk dynamic; by adapting behaviors to fluctuating risk, coyotes might be successfully dampening the amplitude of asymmetry. Integrating behavior with spatial ecology is a worthwhile endeavor and can prove effective in linking causal mechanisms to observed phenomena.

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